



## RESEARCH ARTICLE

# Foredune-forming grass and plant diversity shows contrasting responses along the southeastern United States coast after hurricane disturbance

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## Abstract

**Aims:** Latitudinal gradients in plant communities are well studied, yet how these fundamental ecological patterns influence ecosystem recovery after extreme weather events remains largely unknown. In coastal foredunes, we investigated how the cover of a key dune-building grass (*Uniola paniculata*), vegetation diversity and vegetation cover vary along a short latitudinal gradient during recovery from hurricane disturbance.

**Location:** Southeastern USA.

**Methods:** We surveyed 24 sites, from central Florida to north Georgia (>400 km), four times over 18 months. General linear mixed-effect models were used to unravel patterns of vegetation responses across latitude.

**Results:** Vegetation properties showed countervailing patterns across the latitudinal gradient. While vegetation richness, functional diversity and total cover generally declined, *Uniola* cover increased with increasing latitude. Further, the latitude–richness relationship strengthened while the latitude–functional diversity relationship was invariant with increasing time since the hurricane disturbance. Meanwhile, the latitude–*Uniola* association was seasonally dependent and strongest in the summer. Latitude also influenced diversity–cover relationships: vegetation cover was positively related to species richness at lower latitudes, while it was positively associated with functional diversity only at northern sites. We found no relationship between species richness or functional diversity and increases in cover between time steps; however, recruitment of new species and functional groups was associated with increases in vegetation cover between time steps at northern sites.

**Conclusions:** Our study highlights the temporal dynamism and contrasting patterns along latitudinal gradients exhibited by key engineering species and overall plant diversity in foredunes—a crucial line of coastal protection—exposed to hurricane disturbances. These results suggest a need for greater integration of latitudinal and diversity effects into our understanding of coastal dune resilience. They also highlight

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the potential benefits of enhancing dune plant biodiversity, particularly in areas where the dune-building grasses that are classically employed in restoration (e.g., *Uniola*) are unfavoured, to accelerate the re-establishment of well-vegetated dunes.

#### KEYWORDS

biodiversity, coastal dunes, coastal protection, disturbance ecology, ecosystem functioning, latitudinal gradient, resilience, temporal dynamism

## 1 | INTRODUCTION

Latitudinal gradients in plant communities have been recognized for several hundred years—at least since the observations of von Humboldt early in the nineteenth century (von Humboldt, 1808; Hawkins, 2001)—and remain an enduring topic of study (Cuesta et al., 2017; Gaston, 2000; Lamanna et al., 2014; Willig et al., 2003). While these have been predominantly considered across large scales (thousands of kilometres), even shorter gradients (hundreds of kilometres) can show meaningful changes in climatic conditions and community structure, function and diversity (e.g., Hu et al., 2010; Madritch & Cardinale, 2007; Sun et al., 2009; Stewart & Schriever, 2023). Latitudinal gradients are often considered to be static macroecological patterns (e.g., Gaston, 2000), yet these fundamental gradients may be more dynamic at local community scales, varying, for instance, with season or as ecosystems recover following disturbances (Miller et al., 2010; Shimadzu et al., 2013). Climate change is increasing the incidence and intensity of extreme weather-induced perturbations such as droughts, floods, fires and hurricanes (Woodruff et al., 2013; Dodd et al., 2021; Godfree et al., 2021). Therefore, it is timely to investigate latitudinal gradients in plant communities within the context of ecosystem disturbance and recovery dynamics.

Along latitudinal gradients, environmental changes (e.g., temperature, rainfall patterns) influence multiple properties of plant communities, including diversity and the growth of key ecosystem-engineering species (i.e., species capable of modifying, maintaining and creating habitat; Jones et al., 1994). In many systems, plant species richness and functional diversity decline with increasing distance from the tropics (i.e., increasing latitude, Gaston, 2000; Lamanna et al., 2014; Willig et al., 2003). These diversity metrics can exhibit marked decreases on relatively small scales (hundreds of kilometres) when critical climatic thresholds are crossed (e.g., precipitation and temperature; Cuesta et al., 2017; Di Biase et al., 2021). Conversely, growth properties (e.g., rate of biomass increase) of key ecosystem-engineering species depend on their climatic *optima*; thus, their performance may increase as temperatures decrease with latitude, contrasting with the diversity gradient (e.g., Goldstein et al., 2018; Zvereva et al., 2020). As such, along latitudinal gradients trends of plant diversity may contrast with patterns at the individual (ecosystem engineer) species level, with unknown consequences for ecosystem functioning and potential management implications.

Coastal foredunes are a relevant system to study how plant diversity and ecosystem-engineering species recover after extreme

events such as hurricanes. In the face of extreme storms—and associated surges and waves—foredunes provide a first line of protection to coastal infrastructure, people, homes and businesses (Pries et al., 2008; Houser et al., 2018; Sigren et al., 2018). In foredune systems, dune-building grasses and forbs are integral to the dune's capacity to resist erosion (Bryant et al., 2019; Feagin et al., 2019; De Battisti & Griffin, 2020) while playing a key role in dune formation and growth (Hesp, 2002; Houser et al., 2015, 2018). Site-specific studies highlight that vegetation starts to regrow within a few months of major disturbances (Joyce et al., 2022; Miller et al., 2010), approaching full, geomorphic recovery within three to five years after major hurricanes (Miller et al., 2010; Houser, 2013; Houser et al., 2015). These and other local/site-specific studies also indicate that vegetation composition, anthropogenic disturbance, changes in nutrient retention and sediment grain size and availability can all influence recovery following disturbance (Brantley et al., 2014; Hesp, 2002; Maun, 2009). However, causes of variation in the pace and pattern of foredune vegetation recovery across latitudinal gradients are relatively unknown.

Following storm impacts, the presence and density of key ecosystem-engineering grasses—as well as the diversity of the broader plant community—can dictate both the vegetative and subsequent geomorphic dune recovery. Ecosystem-engineering grasses such as *Uniola paniculata* L. (sea oats, USA; hereafter *Uniola*) and similar analogues (e.g., *Calamagrostis arenaria* (L.) Roth; marram grass, Europe) are renowned for their role in foredune formation and dune recovery and thus, are often the species that are outplanted in dune restoration projects around the world (Pickart, 1997; Hilton, 2006; Maun, 2009). Additionally, plant diversity may play an important role in dune recovery through mechanisms such as niche complementarity and facilitation (Cardinale et al., 2011), as it does in many other vegetated ecosystems (e.g. Klopff et al., 2017). Following disturbance in dunes, plant diversity has the potential to enhance vegetation recovery via stress amelioration by early-successional species, or by serving as a source of recruits from the broader landscape (Loreau et al., 2003). In turn, the broader plant community may also have important geomorphological effects. Past observations indicate that passenger species (*sensu* Stallins, 2005), such as *Cakile maritima* Scop., can nucleate dune formation (Maun, 2009; Hesp, 2002; Ranwell, 1972) and enhance foredune erosion resistance (De Battisti et al., 2019; Feagin et al., 2019). Accordingly, the presence of diverse functional groups of dune vegetation (functional diversity)—rather



than simply the number of species – may be key to enhancing resilience in these eco-geomorphological systems. Yet, despite the possible key roles of engineers and broader plant diversity, few studies have examined how these vegetation properties co-vary and relate to vegetation cover along latitudinal gradients in foredunes recovering from major storm events. Such insights have the potential to advance understanding of why foredunes may vary in space and time in their rate and patterns of recovery as well as inform management and restoration strategies to accelerate dune recovery processes.

Here we report a study documenting plant community recovery in coastal foredunes along the Florida and Georgia coastline in the southeastern United States following hurricane *Irma* in 2017. We specifically investigated how the cover of the primary engineer (*Uniola*) as well as species and functional-group diversity varied with latitude. We hypothesized that dune vegetation properties would show a latitudinal gradient, reflecting changes in winter temperatures: diversity and cover would decline from south to north (i.e., diversity–latitudinal gradient hypothesis), while *Uniola* cover would increase from south to north, reflecting its thermal, fitness optimum. Also, we hypothesized that these latitudinal gradients would strengthen as communities recovered following disturbance. In turn, we explored how these vegetation properties are interrelated across the latitudinal gradient and through time following disturbance, with a particular focus on the potential connection between plant diversity and cover.

## 2 | METHODS

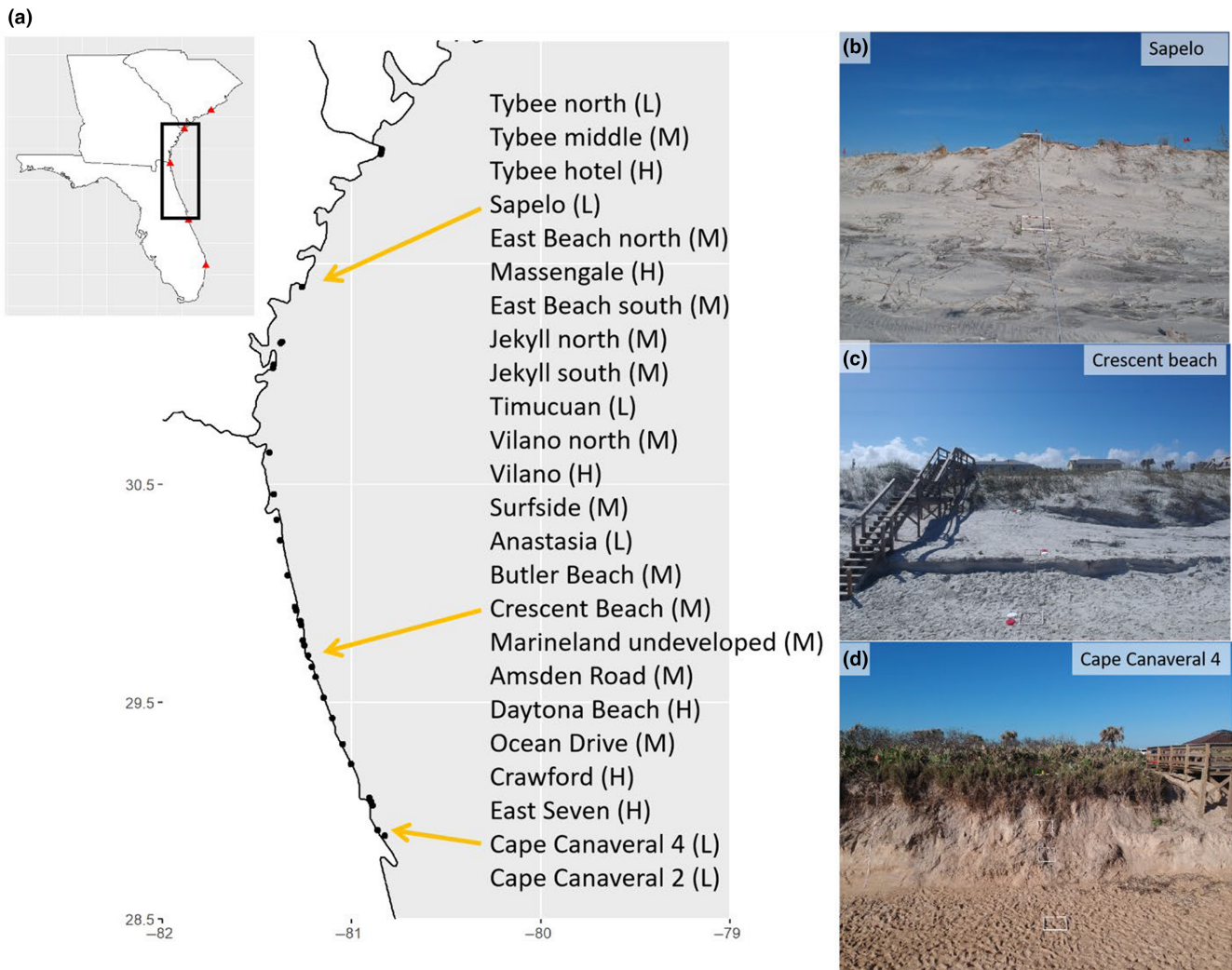
### 2.1 | Study area and site selection

Hurricane *Irma* passed over the Florida Keys as a category-4 hurricane on 10 September 2017 and made landfall in Naples, Florida, at 8pm (GMT) as a category-2 hurricane (Florida Department of Environmental Protection, 2018; Nagarajan et al., 2019; So et al., 2019). Along the eastern coast, the storm surge was high (approx. +2m) particularly between mid-Florida (Trident Pier) and the southern part of South Carolina (Charleston), with the highest storm surge recorded at Fernandina (gauge stations data from NOAA, Appendix S1; So et al., 2019). In February 2018, we identified sites along roughly 400 kilometres of coastline, from Cape Canaveral (Florida; 28.1480°N, –80.1377°E) to Tybee Island (Georgia; 30.0151°N, –80.8414°E), for sampling (Figure 1a). The geographical span of sites was chosen to include a large portion of the coastline affected by this hurricane across different climatic regions, from subtropical (mid-Florida) to more temperate conditions (north Georgia). Despite the relatively short latitudinal span, monthly climatic data obtained from WorldClim (<https://worldclim.org/data/worldclim21.html>) for the period 1970–2000 confirm that latitude correlates strongly with climatic variables (e.g.,  $r = -0.93$  for minimum monthly winter temperature), with sites at lower latitudes being warmer and wetter and having milder winters (Appendices S2 and S3).

Candidate sites (34) were selected based on examination of images from Google Earth (<https://earth.google.com>) prior to arrival and on the following criteria. We identified dunes on ocean-facing beaches (e.g., not within inlets), with reasonable access from a road, and selected sites representing a range of coastal development intensities. In the absence of pre-disturbance vegetation and geomorphological data, we focus here on those factors that were measurable during the post-disturbance period. Development was defined as a three-level factor (Low, Moderate, High). Low development included no development within approx. 1km of the foredune toe, up to a small amount of development (e.g., a minor road) within approx. 100m of the foredune (Appendix S4). These sites were mainly county, state or national parks. Moderate development included sites that had no direct development within the foredune or first swale, but typically had boardwalks for public access or private access from low-density housing situated on the second or third dune ridge (Appendix S4). High development included sites that had buildings located directly on the beach, typically behind small margins of dune (Appendix S4). On our first sampling date, we visually estimated sediment grain size in the field at each site, as a proxy for sediment characteristics (e.g., nutrient retention capacity and sand erodibility; De Battisti et al., 2019) and subsequently quantitatively validated differences in grain size (Appendix S5). We avoided (re-)surveying sites that were undergoing active restoration (e.g., transplantation).

### 2.2 | Vegetation and dune width

At each site, we established three transects, approx. 50m apart, from the highest point on the foredune to the upper beach, which we defined as the most seaward vegetated point. Where possible, transects in each site were surveyed in February 2018, July 2018, January 2019 and July 2019. These dates represent 5, 10, 16 and 22 months after hurricane *Irma*. For logistical reasons, in July 2018, we could not sample eight out of 24 sites (Cape Canaveral 2 and 4, Anastasia, Timucuan, East Beach north and south and Jekyll north and south), while July 2019 sampling followed a slightly modified protocol that is detailed further below. Note that the study duration of 18 months may only capture the initial stages of a longer trajectory of foredune recovery in the absence of further comparable storms. However, relatively short-term recovery trajectories are especially relevant in foredunes as they are dynamic non-equilibrium systems subjected to major periodic disturbances and thus likely to be repeatedly undergoing such disturbance recovery dynamics (Miller et al., 2010). For the first three sampling campaigns, to estimate the cover of all plant species along each transect, a 50 cm × 50 cm quadrat was laid at every metre mark and the percentage cover of each plant species was estimated (Dethier, 1984). To better capture rare or low-abundance species for inclusion in the measure of species richness, we additionally recorded all the plant species present along a wider belt transect, 15m on each side of the original transect.



**FIGURE 1** The distribution of sites sampled along the southeastern coast of the United States during this study (a) and field photos of the foredune observed in February 2018 at the Sapelo (b), Crescent Beach (c) and Cape Canaveral (d) sites. In (a), the development category is indicated in parentheses after each site name such that L refers to low development, M refers to moderate development, and H refers to high-development categories (see section 2 [Methods](#) for description of development categories). Red triangles in the insert of (a) represent the weather and hydrographic stations used to investigate climatic conditions along the investigated area and differences in tidal level during hurricane *Irma* (Appendices [S1](#) and [S2](#)).

To estimate dune width (horizontal distance from the foredune ridge to the foredune toe) and to gain a larger scale and more representative estimate of overall vegetation cover than possible through our quadrat sampling, we used ImageJ (Schindelin et al., 2012) to analyse aerial images of flag-delimited 10-m-wide belt transects obtained using a small unmanned aerial vehicle (UAV; model DJI Spark; Appendix [S6](#)). To estimate vegetation cover from the UAV images, we manipulated image hue and saturation to levels that isolated the vegetation (and standing dead plant material) from the background sand (see Appendices [S6–S7](#) for more details). Total dune vegetation cover was estimated by averaging the vegetation cover across the three transects in each site. In July 2019, we measured species richness and dune width only; on this occasion dune width was measured by calculating the distance between points taken with an RTK GPS from the crest of the dune and dune toe.

To allow quantification of vegetation functional diversity, we categorized species into functional groups following Stallins (2005), based on the capacity of species to influence dune geomorphology: dune builders (DB), burial-tolerant stabilizers (BTS), burial-intolerant stabilizers (BNTS) and passenger species (PS). Only species accounting for at least 1% in cover in at least one site on one date were considered (Appendix [S8](#)). We applied Shannon's diversity index to the functional-group data for computing functional diversity.

### 2.3 | Statistical analysis

All statistical analyses were conducted in R 3.5.2 (R Core Team, 2016). For each sampling date (except July 2019) and site, we averaged the species' percentage cover across the three transects. Although working with site averages reduces the statistical power of the analysis,





we decided to work at the site level because of the difficulty in positioning transects in exactly the same locations within sites through time. To compensate for this, we used a model selection approach to reduce the probability of overfitting (see below) and recognize that the reduced replication would limit detection of weaker effects in our data set. Species were then assigned to each of the four functional groups. We next computed the Shannon diversity index ( $H$ ) on functional groups in each site using the 'diversity' function of the *vegan* package (Oksanen et al., 2019). Through mixed-effect models (*lme4* package; Bates, 2010) to allow for the inclusion of effects of repeated measures through time, we investigated the three following sets of questions:

- I Latitudinal gradients
  - a. How does the cover of the key ecosystem-engineering species, *Uniola paniculata*, vary with latitude?
  - b. How do species richness and the  $H$  of functional groups, two key metrics of plant biodiversity, vary with latitude?
  - c. How does overall plant percentage cover vary with latitude?
- II Relationships between plant diversity and cover
  - a. What is the relationship between plant diversity and overall plant cover, as an indicator of foredune state during recovery?
- III Temporal dynamics
  - a. How do the above relationships change with time as the foredunes undergo post-hurricane recovery?

We tackled these questions using two broad sets of models; the first set (Equations 1–4, see below) tackled question I, examining how vegetation properties varied along latitude and time, and the second set (Equations 5–8, see below) tackled questions II and III, investigating the links between vegetation properties and latitude through time. In the first set of models (questions Ia, b, and c), our main interest was on how *Uniola*, species richness,  $H$  of functional groups, or total vegetation percentage cover (our response variables) varied along latitude through time (fixed categorical variable with three or four levels: February 2018, July 2018, January 2019 and July 2019 for species richness). In these models we also included development (categorical variable with three levels) and grain size (categorical variable with three levels; Equations 1–4 respectively) as covariates. In the species richness model (1), dune width was also included as a covariate as wider dunes are expected to contain more species following the species–area relationship. Latitude–time and development–time interactions were included in all models. We used a model selection approach to reduce the risk of overfitting, using the 'model.sel' function (*MuMin* package; Barton, 2018) to identify which model better described the data (Burnham & Anderson, 2002). For model selection, full models (Equations 1–8) were compared with nested reduced models using maximum-likelihood methods; inspection of the resulting best model(s) was performed refitting the model with the restricted maximum-likelihood method (Burnham & Anderson, 2002). To visualise the results of the mixed-effect models, the package *visreg* (Breheny & Burchett, 2013) was used.

For the first set of models (questions I), the following random-intercept mixed models were fitted to site-level data (full models are shown only):

$$S_{ij} = \beta_0 + \beta_1 L_{ij} * T_{ij} + \beta_2 D_{ij} : T_{ij} + \beta_3 Dw_{ij} + \beta_4 G_{ij} + \epsilon_{ij} \quad (1)$$

$$H_{ij} = \beta_0 + \beta_1 L_{ij} * T_{ij} + \beta_2 D_{ij} : T_{ij} + \beta_3 G_{ij} + \epsilon_{ij} \quad (2)$$

$$U_{ij} = \beta_0 + \beta_1 L_{ij} * T_{ij} + \beta_2 D_{ij} : T_{ij} + \beta_3 G_{ij} + \epsilon_{ij} \quad (3)$$

$$V_{ij} = \beta_0 + \beta_1 L_{ij} * T_{ij} + \beta_2 D_{ij} : T_{ij} + \beta_3 G_{ij} + \epsilon_{ij} \quad (4)$$

where  $S$  is species richness at site  $i$  at time  $j$ ,  $H$  is the Shannon index for functional groups,  $U$  is *Uniola* percentage cover,  $V$  is total vegetation percentage cover,  $L$  is latitude,  $T$  is the sampling date (as a categorical factor),  $D$  is the development level,  $Dw$  is the width of the foredune and  $G$  is sediment grain size. The residuals are assumed to be normally distributed ( $\epsilon_{ij} \sim N, \sigma^2$ ). Note, the symbol '\*' indicates that the main effects and the interaction term have both been included; the symbol ':' denotes that only an interaction term has been included.

In the second set of models (question IIa), we investigated the potential role of diversity in driving vegetation cover through time. Dune vegetation percentage cover was the response variable while latitude, time, species richness,  $H$  and *Uniola* were the predictors (Equations 5 and 6). In these models, we included *Uniola* as a covariate to disentangle the association between cover and biodiversity over that of the key engineering species (i.e., *Uniola*). Development and grain size were included as covariates in all models. In model 5, species richness was log-transformed to account for a non-linear effect of richness on vegetation percentage cover (O'Connor et al., 2017). Latitude–diversity (species richness or  $H$ ) and time–diversity interactions were also included. As in previous models, a random intercept for site was included.

$$V_{ij} = \beta_0 + \beta_1 L_{ij} : S_{ij} + \beta_2 T_{ij} : S_{ij} + \beta_3 U_{ij} + \beta_4 D_{ij} + \beta_5 G_{ij} + \epsilon_{ij} \quad (5)$$

$$V_{ij} = \beta_0 + \beta_1 L_{ij} : H_{ij} + \beta_2 T_{ij} : H_{ij} + \beta_3 U_{ij} + \beta_4 D_{ij} + \beta_5 G_{ij} + \epsilon_{ij} \quad (6)$$

Also, in the second set of models, to further investigate the role of diversity in driving vegetation recovery (question IIIa), we included models where the response variable was the increment in vegetation cover between time points ( $\Delta V_{T_1-T_0}$ , Equations 7 and 8). In Equation 7, the predictors were species richness at time 0 ( $S_{T_0}$ ) and the difference in species richness between two time points ( $\Delta S_{T_1-T_0}$ ), attempting to capture respective processes of diversity of pre-existing species vs arriving species enhancing vegetation growth. Similarly, in Equation 8 predictors were Shannon index of functional groups at time 0 ( $H_{T_0}$ ) and the difference in  $H$  of functional groups between two time points ( $\Delta H_{T_1-T_0}$ ). Both types of models included total vegetation cover at time 0 ( $V_{T_0}$ ) and *Uniola* cover at time 0 ( $U_{T_0}$ ) as covariates. As in Equation 5, species richness was log-transformed. There was now evidence of spatial autocorrelation among sites (Appendix S9).

$$\Delta V_{ij} = \beta_0 + \beta_1 L : S_{T_0ij} + \beta_2 T_{ij} : \Delta S_{ij} + \beta_3 V_{T_0ij} + \beta_4 U_{T_0ij} + \epsilon_{ij} \quad (7)$$

$$\Delta V_{ij} = \beta_0 + \beta_1 L : H_{T_0ij} + \beta_2 T_{ij} : \Delta H_{ij} + \beta_3 V_{T_0ij} + \beta_4 U_{T_0ij} + \epsilon_{ij} \quad (8)$$

### 3 | RESULTS

#### 3.1 | General pattern of dune plant growth after hurricane Irma

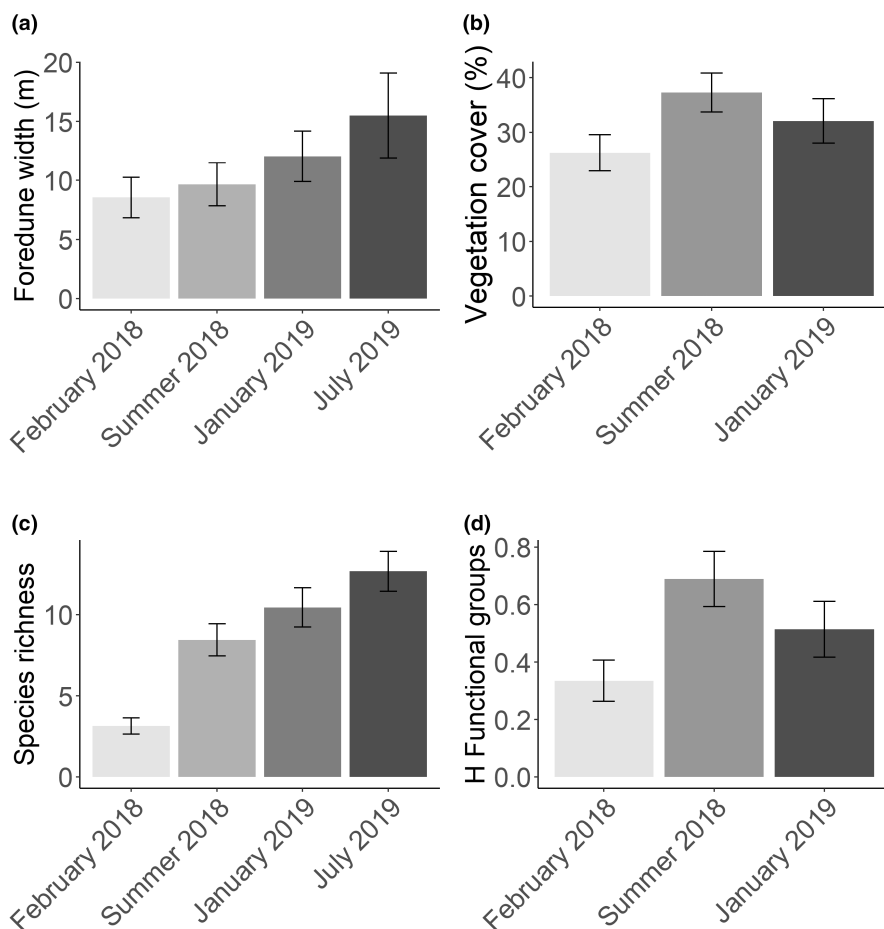
In February 2018, five months after hurricane *Irma*, we conducted the first survey of the 24 sites between Cape Canaveral (FL) and Tybee Island (GA). At this time point, we observed foredunes in a variety of states (Figure 1b–d). While some sites showed evidence of dune scarping, consistent with a recent strong erosion event, others were influenced by sand deposition, indicated by partially buried plants. Overall, foredunes comprised a high proportion of exposed sand, with a limited plant cover (approx. 24% on average). By the end of the study, sites showed a marked regrowth of foredune vegetation (Appendix S10). After nearly an additional year of growth, from February 2018 to January 2019, we observed an approx. 30% increase in foredune width, from a mean ( $\pm$ SE) of  $8.5 \pm 1.6$  m to  $12 \pm 1.8$  m (Figure 2a), while vegetation cover on foredunes increased from  $24 \pm 6\%$  to  $42 \pm 9\%$  (Figure 2b). During the same period, species richness increased from an average of  $3 \pm 0.46$  species per site in February 2018 to  $10 \pm 1$  species in January 2019 (Figure 2c). Functional-group diversity increased 42% in the same period, although a higher increment was evident for the summer period (Figure 2d).

The general trend in recovery through time was also apparent at the site level. In winter 2018, only a few species were present, with

*Uniola* the most abundant species at most sites (e.g., up to 20% in cover in Vilano North, Appendix S11). By summer 2018, vine-type species (burial-tolerant stabilizers) appeared but their abundance decreased during the next winter (Appendix S9). When considering the functional groups (Appendix S11), dune stabilizers (mainly vine types, such as *Hydrocotyle bonariensis* Comm. ex Lam. and *Ipomoea pescaprae* L.) increased in presence and abundance from winter to summer 2018 (up to 10%–15%; Appendix S11). Interestingly, passenger species also increased in presence and abundance through time (up to 10% in cover), yet this group seemed restricted mainly to southern latitudes (Appendix S11).

#### 3.2 | Latitudinal gradients in vegetation community properties

Overall, we found strong support for a latitudinal gradient in species richness, functional-group *H* and the cover of *Uniola*, as well as vegetation cover (first set of models: questions 1a–c; Table 1; full models selection in Appendix S12). Specifically, species richness and functional-group *H* decreased towards northern latitudes (Figure 3a,b; Table 2). Interestingly, these effects strengthened through time for species richness but time did not influence functional-group *H* (time–latitude interaction term had strong support and was statistically significant for species richness, but was not retained in the *H* model;



**FIGURE 2** Changes through time of dune width (a), dune vegetation cover (b), species richness (c) and functional diversity (*H* of functional groups) (d). Note that vegetation cover and functional groups Shannon diversity index (*H* of functional groups) were not sampled in July 2019. Bars represent means with associated standard errors across the 24 sites, with exception of July 2018 where eight sites could not be sampled (see section 2 Methods)



**TABLE 1** Most supported models for Equations 1–8 (full models selection in Appendix S12), selected based on AICc (<2) and weight values

	Models		AICc	Delta AICc	Weight
Equation 1	Response variable	Predictors			
	Species richness	$L^*T+Dw$	342.7	0.00	0.491
		$L^*T+Dw$	343.0	0.35	0.412
Equation 2	$H$ functional groups	$L+T$	35.2	0.00	0.915
Equation 3	<i>Uniola paniculata</i>	$L^*T$	369.4	0.00	0.831
Equation 4	Vegetation cover (%)	$L^*T$	-60.1	0.00	0.746
Equation 5	Vegetation cover (%)	$L^*S+T+U$	-56.8	0.00	0.319
		$L+S+T+U$	-56.2	0.61	0.236
		$L^*S+T+U+G$	-55.8	1.04	0.190
Equation 6	Vegetation cover (%)	$L^*H+T+U+G$	-59.7	0.00	0.268
		$L^*H+T+U$	-58.8	0.86	0.174
		$L^*H+H:T+U+G$	-58.4	1.27	0.142
		$L^*H+T+U+D+G$	-58.2	1.52	0.125
		$L+H+T+U$	-57.8	1.86	0.106
Equation 7	$\Delta$ vegetation cover (%)	$L^*\Delta S+T+V_{T0}+U_{T0}$	-33.7	0.00	0.900
Equation 8	$\Delta$ vegetation cover (%)	$L^*\Delta H+T+V_{T0}+U_{T0}$	-31.1	0.00	0.889

Note: In Equation 5  $S$  was log-transformed. See Appendix S12 for the full model comparison. For Equation 1,  $N=124$ ; for Equations 2–8,  $N=72$ .

Abbreviations:  $D$ , development;  $Dw$ , dune width;  $G$ , grain size;  $H$ , Shannon diversity index of functional groups;  $L$ , latitude;  $S$ , species richness;  $T$ , time;  $U$ , *Uniola paniculata*;  $U_{T0}$ , *Uniola paniculata* at time zero;  $V_{T0}$ , vegetation cover at time zero;  $\Delta H$ , difference in Shannon diversity of functional groups;  $\Delta S$ , difference in species richness between two time points.

Tables 1 and 2). *Uniola* cover also varied with latitude through time (time–latitude interaction term retained and statistically significant; Tables 1, 2), with this dune builder increasing in cover during the summer period particularly at northern latitudes (Figure 3c). Vegetation cover decreased with increasing latitude, but this effect was only present in January 2019 (time–latitude interaction term retained and statistically significant; Tables 1, 2; Figure 3d). Regarding model covariates, neither development nor grain size were retained in any model (Table 1). However, we found clear evidence that wider dunes had more species (Table 2; Appendix S13).

### 3.3 | Relationships between plant diversity and overall cover

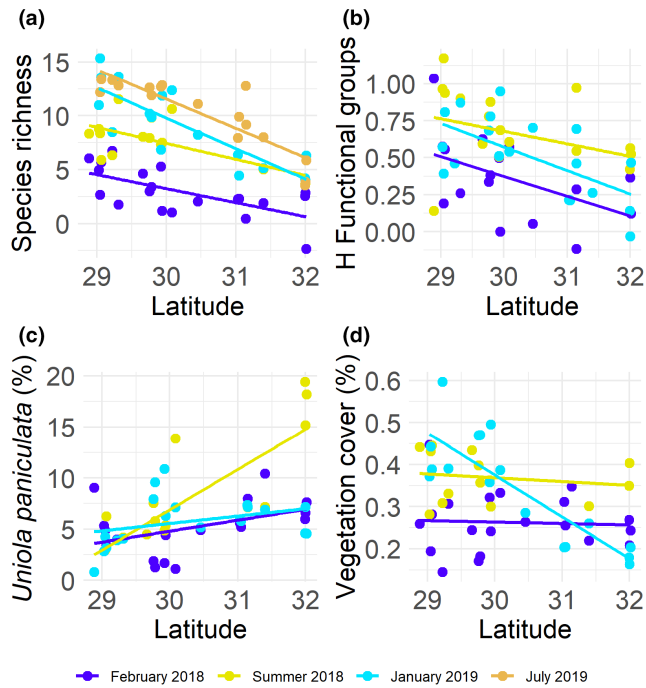
In the second set of models (question IIa, Equations 5 and 6), which investigated the relationship between plant diversity and cover, models with the latitude–diversity interaction, *Uniola* and dune width were the best supported (Table 1). Regarding species richness (Equation 5), inspection of the best models provides good indication for a positive effect of richness on vegetation cover (Figure 4a; Tables 1, 3).

Regarding models with  $H$  of functional groups (Equation 6), we found a clear relationship between this index and vegetation cover, with strong support that this relationship strengthened with increasing latitude (Figure 4b; Tables 1, 3). Less clear was whether the association between  $H$  and cover varied through time; this interaction

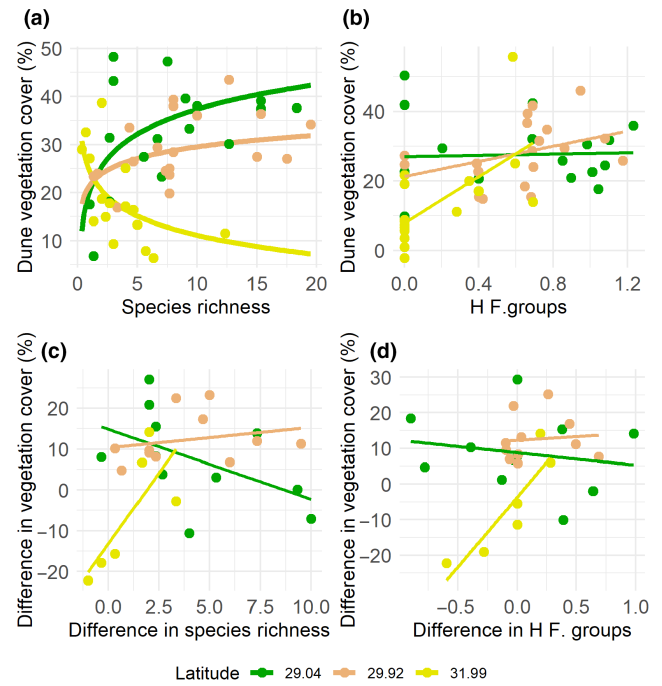
term had some support (Table 1) but inspection of models did not find a significant interaction between  $H$  of functional groups and time. Also, there was some support for a general effect of grain size on vegetation cover (Table 3, with lower cover in sites with finer grain size), but this factor was not always retained in the best models (Table 1). In both model formulations, *Uniola* had a clear relationship with vegetation cover, as sites with high *Uniola* cover support higher vegetation cover (Table 3; Appendix S13).

Lastly, in the second set of models answering question IIIa (Equations 7 and 8), the vegetation increment between consecutive time steps ( $\Delta V$ ; i.e., from one sampling time to a second one) was related to the increase in richness between dates ( $\Delta S$ ), but not to richness at  $T_0$  (not retained in the model, Table 1). Specifically, at lower latitudes  $\Delta S$  had an overall negative relationship with  $\Delta V$ , while at higher latitudes it had a positive relationship (Figure 4c, Table 3). Interestingly, vegetation cover at  $T_0$  had a negative association with  $\Delta V$ , indicating that higher vegetation cover led to lower gains in the following time step (Appendix S13). *Uniola* cover at  $T_0$  did not have a significant effect on  $\Delta V$  (Table 3).

The model with  $H$  of functional groups ( $\Delta H$ ) gave very similar results. The interaction of  $\Delta H$  with latitude was retained in the model but  $H$  at  $T_0$  was not (Table 1). At lower latitudes  $\Delta H$  was not significantly associated with  $\Delta V$ ; however, this relationship became positive and significant towards northern latitudes (Figure 4d). Also, in this model vegetation cover at  $T_0$  had a negative effect on  $\Delta V$ , while the cover of *Uniola* at  $T_0$  had no effect (Table 3, Appendix S13).



**FIGURE 3** Effect of latitude (x-axis) and time (colour-coded points and lines) on vegetation indices, including: species richness (a) and Shannon diversity index  $H$  of functional groups (b), percent cover of *Uniola* key ecosystem engineer (c) and total vegetation cover (d) across sampling dates. Of note, four sampling dates are presented for species richness, but only three for  $H$ , *Uniola* and percentage vegetation cover. The results show the partial residuals of each model against latitude; all models include site as a random intercept (see Appendix S13 for the other covariates included in the model).



**FIGURE 4** Upper plots show the partial residuals of dune vegetation cover depending on species richness (a) and  $H$  F. groups (Shannon index,  $H$ , of functional groups, b) Lower plots show the partial residuals of the difference in vegetation cover between time two steps depending on the difference in species richness (c) or the difference in  $H$  F. groups (d). Species richness is log-transformed. In Latitude, the break points represent the 10th, 50th and 90th quantile respectively. For covariates included in the models see Appendix S13. Models include site as a random intercept.

**TABLE 2** Model results investigating the effect of latitude on vegetation properties

Response variable	Predictor	Sum of squares	Mean square	df	F-value	p-Value	mR <sup>2</sup>	cR <sup>2</sup>
Species richness	Latitude	69.85	69.85	1,20	18.93	<0.001	0.76	0.88
	Time	44.29	14.76	3,49	4	0.013		
	Dune width	176.5	176.5	1,48	47.84	<0.001		
	Latitude:Time	34.74	11.58	3,49	3.14	0.033		
$H$ functional groups	Latitude	0.77	0.77	1,19	12.3	0.002	0.22	0.59
	Time	0.37	0.19	2,35	2.96	0.065		
	Dune width	0.72	0.72	1,27	11.52	0.002		
<i>Uniola</i> cover (%)	Latitude	18.12	18.12	1,19	1.808	0.194	0.12	0.83
	Time	126.51	63.25	2,34	6.312	0.005		
	Latitude:Time	133.08	66.54	2,34	6.641	0.004		
Vegetation cover (%)	Latitude	0.01	0.01	1,17	1.669	0.213	0.21	0.75
	Time	0.11	0.05	2,28	7.772	0.002		
	Latitude:Time	0.1	0.05	2,28	7.56	0.002		

Note: ANOVA tables from the best mixed-effect models retained for Equations (1–4). All models include site as random factor (not shown). In the model for species richness,  $N=96$ ; in other models  $N=72$ .  $H$  functional groups refers to the Shannon diversity index ( $H$ ) of functional groups. Abbreviations: cR<sup>2</sup>, conditional R<sup>2</sup>; mR<sup>2</sup>, marginal R<sup>2</sup>.



TABLE 3 ANOVA tables from mixed-effect models with  $\Delta\text{AICc} < 2$  for Equations 5 and 6 (association between dune vegetation cover and vegetation properties) and Equations 7 and 8 (association between increments in dune vegetation cover and vegetation properties).

Response variable	Predictor	Sum of squares	Mean square	df	F-value	p-value	mR <sup>2</sup>	cR <sup>2</sup>
Vegetation cover	Latitude	11.28	11.28	1,46	0.147	0.703	0.35	0.70
	log(species richness)	437.59	437.59	1,43	5.710	0.021		
	Time	143.22	71.61	2,35	0.934	0.402		
	<i>Uniola</i>	679.74	679.74	1,47	8.870	0.004		
	Latitude:log(species richness)	429.88	429.88	1,43	5.610	0.022		
Vegetation cover	Latitude	814.55	814.55	1,24	8.125	0.009	0.55	0.58
	<i>H</i>	438.61	438.61	1,44	4.375	0.042		
	Time	217.51	108.75	2,30	1.085	0.351		
	<i>Uniola</i>	1596.17	1596.17	1,22	15.922	<0.001		
	Grain	917.31	458.66	1,13	4.575	0.030		
$\Delta$ Vegetation	Latitude	1186.26	1186.26	1,28	18.34	<0.001	0.60	0.60
	$\Delta$ richness	965.58	965.58	1,28	14.92	<0.001		
	Time	0.29	0.29	1,28	0.01	0.947		
	<i>Uniola</i> TO	46.19	46.19	1,28	0.71	0.405		
	Vegetation cover TO	547.39	547.39	1,28	8.46	0.007		
$\Delta$ Vegetation cover	Latitude	960.94	960.94	1,28	14.85	<0.001	0.56	0.56
	$\Delta H$	377.33	377.33	1,28	5.31	0.029		
	Time	778.77	778.77	1,28	10.97	0.002		
	<i>Uniola</i> TO	10.07	10.07	1,28	0.14	0.709		
	<i>Uniola</i> TO	100.06	100.06	1,28	1.41	0.245		

Note: All models include site as random factor (not shown).  $N = 72$  for all models.

Abbreviations: mR<sup>2</sup>, marginal R<sup>2</sup>; cR<sup>2</sup>, conditional R<sup>2</sup>.

## 4 | DISCUSSION

Our results reveal the presence and temporal, post-storm development of latitudinal gradients for vegetation properties in coastal dunes in the southeastern United States. Species richness and vegetation cover both appear to have been sensitive to the major disturbance, showing general increases and development of stronger latitudinal gradients through time following the hurricane. Furthermore, latitude also determined the relationships between vegetation diversity and cover during hurricane recovery, with a positive relationship between species richness and cover evident at southern sites and between functional diversity and cover at northern sites. The arrival of new species or functional groups enhanced cover through time, although only at the less diverse and more seasonal northern sites. Taken together, these results reveal that key vegetation properties and their interrelationships vary with latitude as coastal systems recover from major disturbances, insights with significant implications for the management and restoration of this ecosystem that provides vital storm protection services to coastal communities.

### 4.1 | Ecosystem engineer and plant diversity variation along the latitudinal gradient

In our study, we found a general, positive effect of *Uniola* on dune vegetation cover. Yet, we also found a seasonal latitudinal gradient in *Uniola* cover: in summer, *Uniola* mainly increased in cover at higher latitudes, reflecting enhanced seasonality at the more temperate northern sites. Although our study did not investigate the cause of the seasonal gradient in *Uniola* cover, the result warrants further consideration—particularly the relatively low cover at southern latitudes in both summer and winter. Lower latitude populations of *Uniola* have reduced seed production, approaching zero in Florida at a latitude corresponding to our southern sampling sites (Cape Canaveral 4, 28.88° N; Colosi, 1979; Hester & Mendelssohn, 1987, 1989). One possible explanation is that more southern sites may lie closer to the water table, potentially due to lower-elevation dunes and greater precipitation (Appendix S3); experimental studies have demonstrated that *Uniola* strongly suffers from inundation or a high water table (Hester & Mendelssohn, 1989; Mullins et al., 2019). Another possibility is that reduced seasonality enhanced the

growth of other species, increasing competitive effects on *Uniola*. Considering the key role that this species has in driving dune growth, recovery and erosion resistance (Maun, 2009; Hooton et al., 2014; Feagin et al., 2019), our work highlights the need to further investigate the consequences that this latitudinal gradient might have on the dune resilience against increasing storm frequency and strength (Woodruff et al., 2013).

In contrast to the pattern observed for the key engineer *Uniola*, and in accordance with the large literature on the latitude–diversity relationship (e.g., Gaston, 2000; Hawkins, 2001; Willig et al., 2003), we found that both species richness and functional-group diversity declined towards higher latitudes. Across systems, the reduction in richness towards northern areas has been mainly linked to changes in climatic conditions, such as snow and frost formation in winter, a shorter growing season, or changes in precipitation regimes (Cuesta et al., 2017; Johnson, 1982; Keddy & Laughlin, 2022). For instance, coastal dunes of the east coast of Mexico Bay showed a decreasing richness gradient from southern, wetter areas, to northern, drier areas (Johnson, 1982). Similarly, the colder, drier climate of northern sites in our study may be (at least partially) responsible for the latitude–richness relationship. Yet, when checking the literature for broad geographical distributions of the species found here (see Appendix S14), we did not find a clear threshold for their presence/absence along our study area. Perhaps, climatic conditions in northern sites acted on the abundance and occupancy of species, reducing the probability of them occurring in sampled patches, or restricted them to less environmentally harsh back-dune or upland habitats. Our measurement of functional diversity also indicates latitudinal shifts in the diversity and composition of vegetation assemblages. Specifically, there is a lack of burial-intolerant stabilizers (BNTS) and a lower presence of passenger species (PS) in the northern sites, while the dune builder group (DB, mainly comprising *Uniola*) increases in dominance.

Reduced species richness and functional diversity, as well as changes in functional-group composition, at a local scale have potential implications for ecosystem functions and services (Isbell et al., 2015; Ford et al., 2016; Fairchild et al., 2018). This includes dunes' sensitivity to overwash regimes (i.e., DB species dominance leads to tall foredunes, reducing the chance of overwash, while BTS dominance has the opposite effect; Stallins, 2005) and indicates important changes in the structure of plant communities along the latitudinal gradient. Furthermore, considering the role played by vegetation cover in dune recovery (Houser et al., 2015, 2018), it is surprising how little is still known about how diversity and key ecosystem engineers vary in abundance with latitude. We stress that more research is required to understand how covariation between diversity and ecosystem-engineering species influences ecosystem functioning and services in sand dunes and other systems.

Lastly, we were surprised that urban development and sediment grain size had no or very little influence, respectively, on diversity indices or *Uniola* and vegetation cover. Regarding development, it is worth noting that sites with highest development were also those

with the smaller dune width (e.g., Daytona beach). Thus, considering that dune width was strongly positively associated with species richness and that in turn this had a positive relationship with vegetation cover, our results suggest that development could indirectly impact on the recovery of foredunes. With respect to sediment grain size, we can only speculate that at this large scale of investigation other factors such as climatic variation held primacy over grain size and associated nutrient availability. It should also be noted that the large-scale and site-scale grain of our sampling inevitably constrained sample size and therefore the power of our statistical analyses to detect more subtle drivers or interactions among drivers. Future studies may gain enhanced power to detect such drivers by constraining variation (e.g. comparing low- and high-development sites within a region), or undertaking large-scale efforts coordinated across multiple geographically distributed research groups.

## 4.2 | Dune vegetation cover and implications for dune resilience and for sand dune management

In this study, on top of the expected positive relationship between *Uniola* and vegetation cover, we also found positive relationships between diversity and vegetation cover. Interestingly, latitude modulated this relationship for both species richness and functional-group diversity. A positive relationship between plant diversity and vegetation cover or biomass is known in other systems (Reich et al., 2001; Steudel et al., 2011; Hong et al., 2022) and has previously been demonstrated experimentally in sand dunes (Long et al., 2013). We show here that diversity–cover relationships can depend on latitude and on the facet of diversity considered, pointing to the complexity of diversity–cover relationships on large scales in coastal dunes.

The finding that *Uniola* does not thrive at the southern edge of this latitudinal gradient has crucial implications for sand dune management. In Florida, although the prevailing strategy to restore sand dunes, particularly after hurricane damage, focuses on outplantings of *Uniola*, restoration manuals also highlight the importance of employing a large array of species (Miller et al., 2018). Our findings indicate that the efficacy of planting a monoculture vs multiple species likely varies strongly with latitude. Accordingly, in southern areas managers should favour planting a more diverse array of species, mimicking the natural dune recovery trajectory, to enhance restoration success. More generally, managers need to be aware of the possibility that long-recognized foundation species used widely in coastal restoration may be complemented by a more diverse array of species towards their equatorial distributional limits.

Despite intriguing diversity–cover relationships, we were not able to tie vegetation diversity to the subsequent increase in cover between time points, as is expected based on biodiversity–ecosystem functioning theory via mechanisms such as complementarity and selection effects (Cardinale et al., 2011). This suggests that diversity and cover increased together to the south and with time after disturbance, or a third unmeasured factor, and that there was



not necessarily a causal effect of diversity on cover. It may also be that the causal relationship is reversed such that higher cover enhances richness and diversity through more individuals (i.e., species accumulation effects), or facilitation. That said, we did find evidence that seasonal (winter to summer) increases in species and functional diversity led to greater increases in cover at more northern sites; accordingly, the diversity–function link may be mediated by seasonal recruitment/growth of diverse species that in turn increase cover in the summer at the more seasonal and lower-diversity northern sites. Therefore, our study suggests that key ecosystem-engineering species (e.g., *Uniola*) might not exclusively be responsible for the recovery of foredunes after extreme weather events, but that diversity possibly plays a complementary, yet poorly recognized and context-dependent role.

As plant diversity increased towards the south, while the key engineer declined, it could be argued that plant diversity may functionally compensate for the latitudinal decline in *Uniola*, maintaining dune resilience. However, morphological differences among plant species can influence sand deposition patterns (Hacker et al., 2019; Hesp et al., 2019), potentially shifting foredunes from being resistant to storms but slow to recover, to foredunes less resistant but quick to recover (Wolner et al., 2013; Houser et al., 2015; Patrick et al., 2022). Therefore, although high species diversity might compensate for the decline in *Uniola* cover at lower latitudes, the changes in the community traits may still impair the overall resilience of foredunes (Pries et al., 2008; Wolner et al., 2013). More research, including crucially experimental manipulations (see Long et al., 2013) are needed to understand the possible role of diversity in dune vegetation cover, growth and post-hurricane recovery and how that role varies with latitude.

## 5 | CONCLUSION

In conclusion, our study provides important insights into the presence and temporal evolution of latitudinal gradients in coastal dunes, even over a relatively short latitudinal gradient, with broader implications for recovery and management. We show the strengthening of the latitude–richness relationship through time following a hurricane event and further reveal the opposing directions of latitude–richness and latitude–engineer relationships. Meanwhile, our results also highlight a role of latitude in moderating the relationship between plant diversity and cover, pointing towards intriguing roles of different facets of plant diversity in supporting dune resilience at different latitudes. This result may have valuable implications for management and restoration. Planting key ecosystem-engineering species in monoculture, a practice largely utilized in foredunes and other systems, may or may not be effective depending on latitude. Overall, our study reveals the dynamism and interconnectedness of latitudinal gradients in vegetation properties following large-scale disturbances in coastal foredunes and underlines that disturbances must be integrated into our understanding of latitudinal patterns in these critically important systems.

## AUTHOR CONTRIBUTIONS

Davide De Battisti, John Nicholas Griffin and Christine Angelini conceived the idea; Davide De Battisti, John Nicholas Griffin, Matthew Joyce, Tom Phillip Fairchild, Sinead Crotty and Hallie Samantha Fischman collected the data; Davide De Battisti analysed the data; Davide De Battisti and John Nicholas Griffin led the writing with contribution of all authors. John Nicholas Griffin and Christine Angelini secured the funding.

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## CONFLICT OF INTEREST STATEMENT


The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings are available at: [10.6084/m9.figshare.24798789](https://doi.org/10.6084/m9.figshare.24798789).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1.** Table reporting the highest astronomical tide (HAT) along the southeastern coast of the United States (including the sites sampled in this study) within each year (2017–2019).

**Appendix S2.** Average temperature and precipitation data along the southeastern coast of the United States (including the sites sampled in this study) for the period 1940–2020.

**Appendix S3.** Climatic conditions along the latitudinal gradient included in our study.

**Appendix S4.** Landscape and high-shot images of examples of foredunes.

**Appendix S5.** Sediment grain size validation.

**Appendix S6.** Drone image acquisition.

**Appendix S7.** Validation method for dune width measurements using UAV images.

**Appendix S8.** Plant species with more than 1% in cover found within quadrat.

**Appendix S9.** Cover of species and functional groups across sites in different time sampling periods.

**Appendix S10.** Model selection results for Equations 1–8.

**Appendix S11.** Geographical records of the species found in our study.

**Appendix S12.** Semivariograms of models 1 to 8 respectively, for detecting possible spatial correlation patterns.

**Appendix S13.** Examples of foredune vegetation recovery.

**Appendix S14.** Partial regression plots of models from Equations 1, 5–8.

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